

Long-Term Trends in Burbot Abundance in Oneida Lake, New York: Life at the Southern Edge of the Range in an Era of Climate Change

JAMES R. JACKSON*, ANTHONY J. VANDEVALK, AND JOHN L. FORNEY
*Department of Natural Resources, Cornell Biological Field Station
900 Shackelton Point Road, Bridgeport, New York 13030, USA*

BRIAN F. LANTRY
*U.S. Geological Survey Biological Resources Division (USGS)
Lake Ontario Biological Station, 17 Lake Street, Oswego, New York 13126, USA*

THOMAS E. BROOKING AND LARS G. RUDSTAM
*Department of Natural Resources, Cornell Biological Field Station
900 Shackelton Point Road, Bridgeport, New York 13030, USA*

ABSTRACT.—The burbot *Lota lota* is a cold-stenothermal species with a circumpolar distribution that rarely extends below latitude 40°N. Oneida Lake, New York, is a large (20,670 ha), shallow (mean depth 6.8 m) lake and its position at latitude 43°N places it near the southern border of the burbot's range. Although abundant enough to be considered detrimental to more desirable species during the early 1900s, previous research indicated that burbot abundance was limited by sea lamprey *Petromyzon marinus* predation and marginal thermal conditions during the summer in Oneida Lake. However, a lamprey control program initiated in 1985 did not result in significant increases in burbot catches. Oneida Lake's morphology results in homothermal conditions throughout much of the summer, reducing the availability of coldwater refuges. High occurrence of empty stomachs and reduction in energy density of livers during the summer months suggest that high summer water temperatures may limit burbot in Oneida Lake. Long-term trends in catches of burbot in bottom trawls, gill nets, and trap nets since the 1960s have exhibited significant declines. During the same period, summer water temperatures have increased significantly. Bioenergetics models suggest that water temperatures greater than 21°C will result in weight loss in burbot, and the average duration of this period of high summer stress has increased to almost 2 months in recent years. Declines in burbot catches were significantly correlated with increases in summer temperatures and the number of days when weight loss was predicted by energetics models. Continued warming of Oneida Lake may result in extirpation of this burbot population.

Introduction

The burbot *Lota lota* is the only true freshwater representative of the cold-stenothermal

marine family Gadidae (Hölker et al. 2004). It is characterized by a circumpolar distribution with a southern limit that correlates with the coverage of the Wisconsin ice sheet and only rarely reaches latitudes as far south as 40°N (Cohen et al. 1990; Howes 1991). While

* Corresponding author: jrj26@cornell.edu

Hölker et al. (2004) show that the burbot has adapted to some degree to the higher temperatures encountered seasonally in freshwater habitats, preferred temperatures have been reported in the range of 11.4–14.2°C, and at the southern extent of their range, burbot are restricted largely to deep lakes or cool rivers at higher altitudes (McPhail and Paragamian 2000; Hölker et al. 2004). Little attention has been paid to the population dynamics of burbot in marginal habitats at the southern extent of their range. Their sensitivity to prolonged periods of high temperatures make southern burbot populations a potential indicator for fish community changes and range contractions of coldwater species predicted in light of current trends in global climate change (Stefan et al. 2001; Hölker et al. 2004).

New York State represents the southern extent of the range where burbot populations can be found in inland lake habitats in eastern North America (Robins and Deubler 1955). Historically, the burbot was reported as abundant in deeper New York lakes such as Canandaigua Lake, Otsego Lake, and Lake Champlain, as well as in the upper reaches of the Allegheny and Susquehanna River systems (Bean 1903; Robins and Deubler 1955). While the presence of burbot in the deeper lakes of New York is consistent with the habitats they occupy elsewhere in the southern parts of their range, the burbot is also found in Oneida Lake, a large, shallow lake in the lake plains region of central New York.

The fisheries of Oneida Lake have been a regionally important economic resource since the area was first inhabited by Native Americans, continuing through the period of European settlement and into the modern era. Reports on the fisheries featured prominently in early travelers' accounts. By all accounts, burbot were common in Oneida Lake, but not held in high regard. DeWitt Clinton's journal from a July 1810 trip across the lake provides the first clear report of burbot, along with an

indication of local opinions about the fish (from Campbell 1849): "our men speared several fish in it [Scriba Creek on Oneida Lake's north shore] – among others, one eighteen inches long, spotted, the head like a cat-fish, and downwards like an eel, but a dog-fish in shape. Some called it an eel-pout, and others a curse."

Early fisheries investigations on Oneida Lake provided more definitive indications that burbot were quite abundant in the lake and confirmed that they were considered more as a threat to desirable species than as a resource. Adams and Hankinson (1916), in an early report on the fisheries of Oneida Lake, reported that burbot were taken in large numbers in trap nets. In a more comprehensive report, Adams and Hankinson (1928) reiterated reports from trap-net fishermen and local fish market operators of the abundance of burbot in Oneida Lake. They also noted the damage burbot predation could have on "high grade" fish in the lake and provided evidence of the prejudice against burbot held by local anglers: "large numbers are said to be taken by tip-up fishermen...Frequently the Lings are left on the ice...There are reports of substantial windbreaks being made of the carcasses of these Lings during ice fishing." Other fisheries investigations in the region echoed the view of burbot as a "menace to better food fish," and advocated employment "of any means which would reduce its numbers without serious damage to other fish..." (Eaton 1928).

Quantitative data on the burbot population in Oneida Lake were not collected until establishment of the Cornell Biological Field Station in the mid-1950s. As a result of intensive studies of fish populations in the lake, records of burbot catches, at both larval and adult stages, were initiated. Clady (1976) reported on the distribution and abundance of burbot larvae during the years 1965–1975. He observed densities of larval burbot sam-

pled by Miller high-speed samplers that approached those recorded for yellow perch *Perca flavescens*, despite low catches of adult burbot in gill nets and trap nets relative to catches of yellow perch (larval burbot densities ranged from 6 to 71/100 m³ over the course of Clady's study). He hypothesized that the relative abundance of larval burbot indicated high survival of eggs and prolarvae during the winter and spring months.

Based on his observations of burbot dynamics, Clady (1976) speculated that the high survival of early life stages of burbot could act to maintain the population in spite of suboptimal temperature conditions during the summer and heavy parasitism of adult burbot by sea lamprey *Petromyzon marinus*. Sea lamprey had been identified as a significant source of mortality for Oneida Lake's fishes since the early decades of the 1900s (Forney 1986). Forney (1986) found that sea lamprey attacks were disproportionately high in the lake's coldwater species, the burbot and cisco *Coregonus artedii*, and concluded that sea lamprey-related mortalities could have played an important role in controlling the abundance and population dynamics of these species. Lamprey control was initiated in Oneida Lake in 1985 and effectively reduced the lamprey population to negligible levels. As lamprey control had allowed expansion of burbot populations in the Great Lakes (e.g., Fratt et al. 1997), there was concern that once released from lamprey predation, Oneida Lake's burbot population would expand to levels that could present a threat to game fish.

The objective of the current manuscript is to assess long-term trends in burbot abundance in Oneida Lake in relation to summer water temperatures, a key habitat limitation for burbot in Oneida Lake. Implications of long-term changes in temperature conditions are examined through the use of a bioenergetics model and related to observations

on seasonal patterns in diet and condition of burbot.

Study Site

Oneida Lake, the largest lake wholly within New York State's borders, lies in the Lake Ontario Plain centered at latitude 43.2°N and longitude 75.9°W. The lake is 33.6 km long, averages 8.8 km wide, and has a surface area of 20,670 ha. Oneida Lake is a remnant of the Pleistocene-era Lake Iroquois and is one of numerous undrained depressions left behind as glaciers retreated at the end of the last ice age (Mills et al. 1978). The lake is shallow, with an average depth of 6.8 m (maximum depth 16.8 m), with numerous shoals, resulting in some 26% of the lake bottom being shallower than 4.3 m. Oneida Lake's west-northwest to east-southeast orientation is fully exposed to prevailing winds, which, combined with its long axis, results in homothermal conditions throughout most of the summer. Thermal stratification may develop during prolonged calm periods, but rarely persists (Mills et al. 1978). Historically, Oneida Lake was highly productive, nutrient levels being fed by decaying organic matter in surrounding wetlands prior to development of the area and later by phosphorus loading from domestic and agricultural sources. Nutrient input reductions in recent decades have resulted in a shift to a more mesotrophic state.

Methods

Data Collection

Research on Oneida Lake has been ongoing since the mid-1950s and has included long-term monitoring of both the fish community and limnological parameters. While sampling protocols for most fish population assessments were developed to target walleye *Sander vitreus* and yellow perch, burbot have been commonly captured in several gears, es-

establishing a foundation for assessing trends in burbot abundance over the course of the last five decades (see Forney 1980 for a review of percid research on Oneida Lake).

Long-term trends in larval burbot abundance were assessed using Miller high-speed samplers with a 10-cm mouth and fitted with 530- μ m-mesh nylon nets towed at 3.6 m/s (Noble 1970). Surveys each year were conducted 8–10 d following stocking of walleye fry by the Oneida Fish Cultural Station, typically mid-May. For each survey, sampling was conducted at 46 randomly selected sites using four simultaneously towed Miller samplers distributed to sample multiple depth strata. Distance towed at each site was approximately 1.6 km. Data from surveys conducted under these protocols were available for the years 1966–1967, 1969–1974, 1976, 1992, and 1998–2005.

Burbot catches from spring bottom trawling, summer gill netting, summer–fall bottom trawling, and fall trap netting were used as independent indices of adult abundance through the time series. Spring trawl samples were collected on two to three dates each year centered on May 1, using a bottom trawl with a 5.5-m footrope and constructed of 39-mm stretch mesh in the body and 13-mm mesh in the cod end. Each sample consisted of one haul at a speed of 3.4 km/h at each of 10 fixed sites, with each haul sweeping approximately 0.1 ha (Nielsen 1983). Spring trawl samples were available for all years from 1964 to 2005, excepting 1968, 1979–1980, and 1982. Annual summer gill-net surveys were conducted using a 183-m-long by 1.8-m-deep multifilament experimental gill net set on bottom. The gill net consisted of four gangs, each 45.8 m long and composed of six 7.6-m panels with mesh sizes ranging from 38- to 102-mm stretch mesh in 12.7-mm increments, resulting in four complete series of mesh sizes. Annual surveys included overnight sets at each of 15 fixed sites, with 1 site

sampled each week from early June through mid-September in the same order each year. Nets were set at approximately sunset and retrieved at about 0730 hours, with time fished standardized for each location each year. Gill-net surveys were conducted in all years from 1958 to 2005 except 1974. Summer–fall bottom trawling was conducted weekly from July through October using the same trawl and sampling protocols described for spring trawling (see above). Fall trap-net surveys were conducted at one site each year using a net design introduced to Oneida Lake by early settlers (Kingsbury 1964; also reproduced in Forney et al. 1994). The net consisted of a 1.8 \times 1.8 \times 1.8-m crib, outside and inside wings with a combined length of 12.8 m, and a first heart with turnaround that led into a second heart with turnaround that funneled into a third heart in the crib. The net utilized a 45.4-m lead, and all sections were constructed of 25.4-mm-bar-mesh multifilament netting. The net was typically fished 7–10 d in October each year and tended daily or as weather permitted. Trap-net survey data were available for the years 1959–1962, 1980–1981, 1983–1984, 1986–1989, and 1991–2005.

Data for assessment of trends in growth, feeding, condition, and liver energy content of adult burbot were collected primarily during the late 1970s through the early 1990s. All adult burbot captured were measured in total length (mm) and weighed (g). Ages were determined from otoliths for burbot captured in trap nets from 1976 to 1994 (Martin 1941). Stomach contents were examined from adult burbot captured in gill nets, trawls, and electrofishing from 1975 to 1994, with diet items broadly classified as invertebrates or fish. Identifiable fish in burbot diets were enumerated by species and classified as young of year or older. Seasonal trends in liver energy content were examined in 1993 and 1994. A sample of 10 livers from spring 1993 and 5 livers from fall 1994 were weighed and ana-

lyzed for caloric content using oxygen-bomb calorimetry (Phillipson 1964). Livers were diced and dried at 60°C. Oil was collected from each liver during the drying process and weighed. After drying was completed, water content was determined by weight loss, and samples were homogenized using a blender and mortar and pestle, then redried. Two samples (approximately 5 g each) were then taken from each liver for use in energy determinations using a Gentry Instruments microbomb calorimeter following the guidelines of Phillipson (1964). Energy content was calculated by multiplying the mean energy density by the dry weight and adding the caloric value of the oil removed from each sample (9,430 cal/g; Wootton 1990).

Water temperatures during the ice-free season in Oneida Lake have been monitored at a fixed site near the central south shore of the lake since 1968. Temperature readings were collected at a depth of 10 m, which in Oneida Lake is likely representative of the deeper habitats utilized by burbot. Daily temperature readings were collected from 1968 to 1988 using chart recorders that were calibrated weekly using a thermistor reading. From 1989 to 1993, temperatures were logged continuously using Ryan Tempmentors, and Onset temperature recorders have been used from 1994 through the duration of this study. Daily temperature means were used to calculate mean monthly water temperatures for the hottest months (July, August, and September). Additionally, for all years, we calculated total number of days when mean water temperature exceeded critical temperatures as determined through bioenergetics modeling (see below).

Analyses

Time trends in burbot catches as a function of year were examined using simple linear regression. Because catch data were not normally distributed, catches were log-trans-

formed prior to analysis [$\log_{10}(\text{catch} + 1)$]. Because our sampling protocols were standardized, catch data for gears such as gill nets were technically discrete data and did not meet the assumptions of linear regression. However, when distances between observed values are small relative to the range of possible values, this violation of assumptions is typically not of concern, so we used linear regression in all our catch analyses (Hayek and Buzas 1997). Time trends in summer water temperatures at 10 m depth were also examined by linear regression of temperature as a function of year. As with some of our catch data, counts of days above critical temperatures were discrete data, but the range of observed values was large relative to the potential distance between observed values, so we used linear regression for these analyses as well. A criterion for significance in all tests was established at the level of $\alpha \leq 0.05$.

To examine the potential relationship between long-term trends in water temperatures and burbot catches, we used simple linear regression of log-transformed catch as a function of mean August water temperature at 10 m depth (August was chosen because it is typically the month with the highest water temperatures and therefore represents the time of greatest potential thermal stress for burbot). Given that the sublethal influence of thermal regimes on burbot dynamics would most likely be a function of cumulative effects over multiple years, we used running averages of water temperatures for these analyses. We followed conventions of the growing body of literature on global climate change (e.g., Hansen et al. 1999) and used 5-year running averages for our analyses (e.g., burbot catch in the year 2000 was regressed against the average water temperature for the 5 years ending in 2000). Because we conducted multiple tests of the relationship between burbot catches (four different gears) using a single independent variable (water temperature), we

adjusted the acceptance level for significance to correct for Bonferroni's inequality ($n = 4$ tests, adjusted $\alpha = (0.05/n) = 0.013$; Snedecor and Cochran 1980). Decisions regarding analyses to conduct were made a priori and all results are presented.

To assess the potential influence of summer habitat conditions on burbot feeding and energy dynamics, we used bioenergetics modeling. Temperature-dependent feeding and metabolic rates (in g/g/d) for a 1-kg burbot were calculated using the equation developed by Kitchell et al. (1977) and model parameters for burbot developed by Pääkkönen et al. (2003). These rates were then used to determine the temperature at which energetic costs (metabolism and wastes) would exceed intake from feeding (e.g., Figure 1 of Hanson et al. 1997). Influence of summer temperatures was further assessed by comparison of length-weight relationships of burbot before and after the summer, as well as assessments of condition using relative weights calculated with the equation proposed by Fisher et al. (1996).

Results

Catches of adult burbot in all gears were highly variable among years, but trends across the time series reflected declining catches, particularly over the last 10–15 years (Figures 1 and 2). Linear regression analyses revealed highly significant declines in catches with time for spring trawling ($r^2 = 0.30$, $df = 36$, slope = -0.009 , $P = 0.0004$), summer gill netting ($r^2 = 0.33$, $df = 45$, slope = -0.013 , $P < 0.0001$) and summer–fall trawling ($r^2 = 0.28$, $df = 44$, slope = -0.001 , $P = 0.0002$). Fall trap-net catches did not exhibit a significant time trend ($r^2 = 0.09$, $df = 25$, slope = -0.008 , $P = 0.12$). Catches of larval burbot in Miller high-speed samplers were also highly variable among years, but 60% of the samples collected since 1990 were below the long-term mean while 78% of those collected prior

to 1976 were at or above the mean (Figure 3). However, the decreasing trend in larval catches across time was not significant ($r^2 = 0.14$, $df = 17$, slope = -0.01 , $P = 0.12$).

Length-at-age data indicated that burbot growth rates in Oneida Lake are slow relative to most populations for which similar data are available (Figure 4). Growth rates in Oneida Lake after age 5 were slow, and the largest burbot recorded was 678 mm at age 10. Growth rates in Oneida Lake were significantly slower than reported from populations in upper Red Rock Lake, Montana (Katzman and Zale 2000; test for homogeneity of slopes of linear regressions of length as a function of age: $df = 1$, $F = 29.22$, $P < 0.001$), Lake Simcoe, Ontario (McCrimmon 1959; $df = 1$, $F = 22.84$, $P = 0.001$), and Lake Erie (Clemens 1950b; $df = 1$, $F = 22.54$, $P = 0.001$). Length-at-age for younger burbot in Oneida Lake was greater than reported for another southern population from Lake Winnebago, Wisconsin, but rapid growth of older fish in Lake Winnebago resulted in an overall faster growth rate (Weber 1976; $df = 1$, $F = 72.42$, $P < 0.001$). Burbot catches in Oneida Lake since the early 1990s were too low to facilitate assessment of potential time-trends in growth rates.

Summer water temperatures at a depth of 10 m have increased in Oneida Lake over the past several decades (Figure 5). Water temperatures for the summer months have exceeded long-term averages most years since the early to mid-1990s, concurrent with trends in declining burbot catches. Water temperatures exhibited significant increasing trends for July–September over our 37 year data set (July: $r^2 = 0.30$, $df = 32$, slope = 0.06 , $P < 0.0008$; August: $r^2 = 0.29$, $df = 33$, slope = 0.05 , $P < 0.0009$; September: $r^2 = 0.13$, $df = 33$, slope = 0.04 , $P = 0.03$). Linear regression indicated that adult burbot catches were negatively correlated with 5-year running average August water

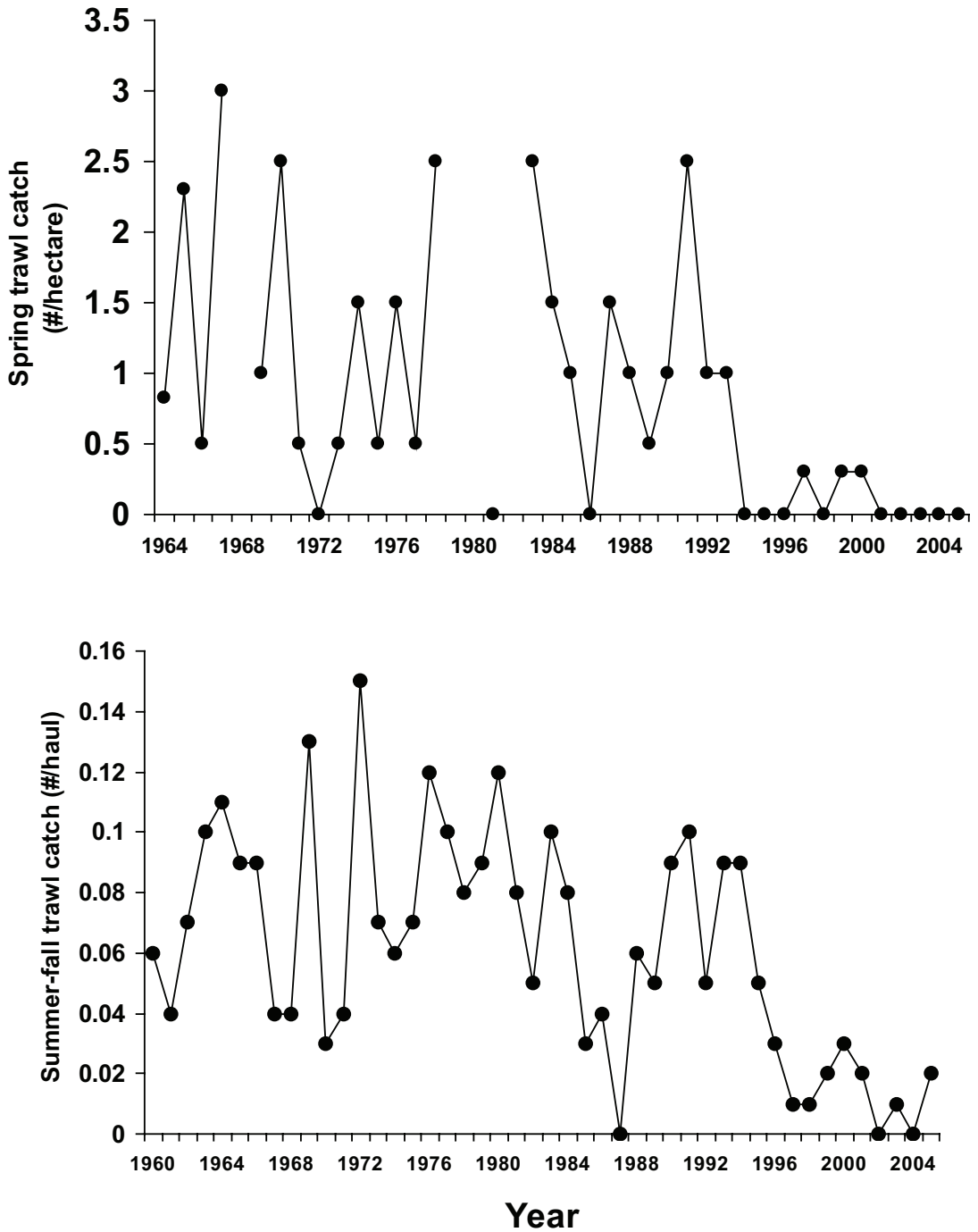


FIGURE 1. Catches of adult burbot in spring and summer-fall bottom trawl surveys, in Oneida Lake, New York, 1957–2005.

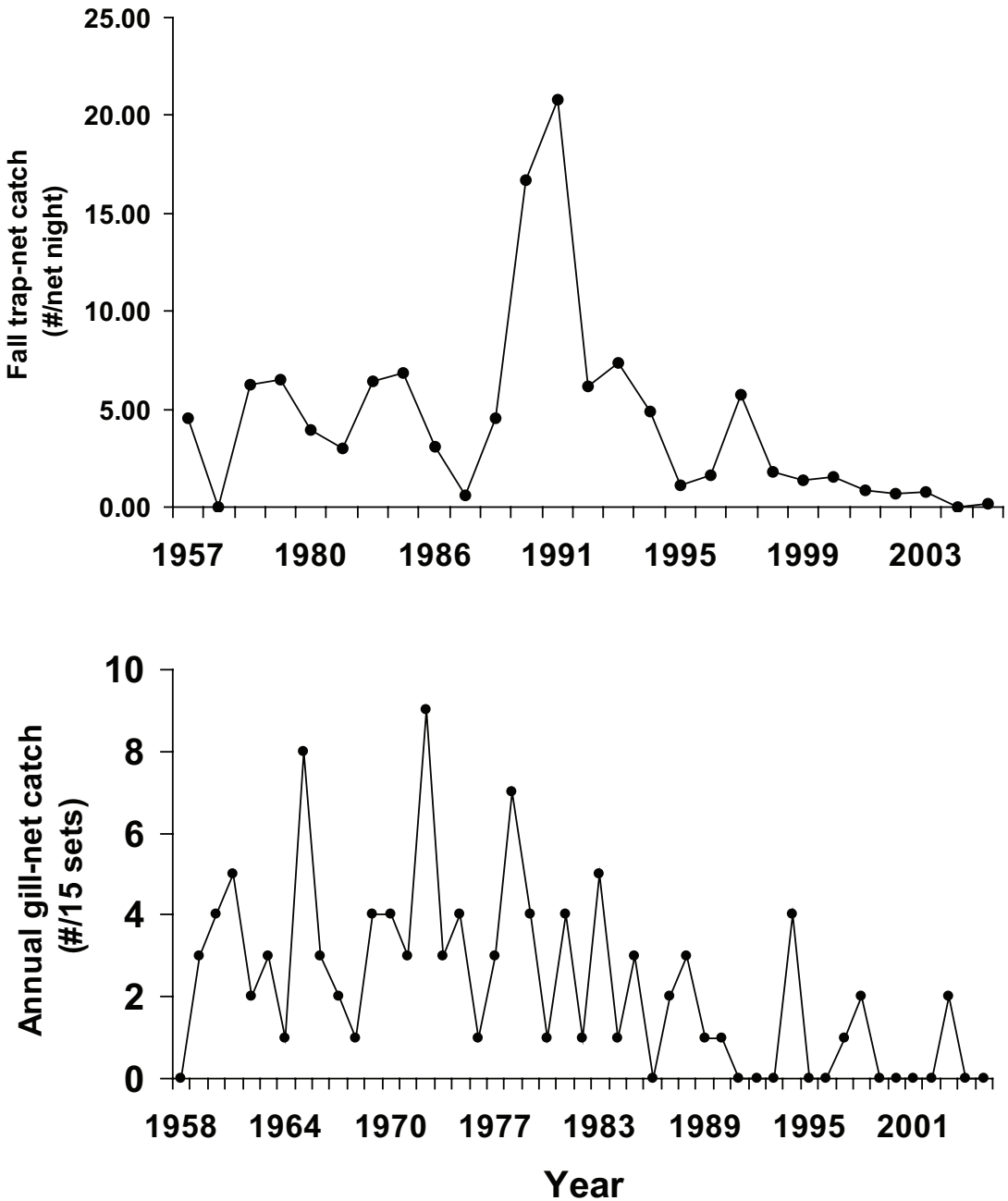


FIGURE 2. Catches of adult burbot in fall trap-net and summer gill-net surveys, Oneida Lake, New York, 1960–2005.

temperatures and all tests were significant at the adjusted level of $\alpha = 0.013$ for all gears (spring trawl: $r^2 = 0.24$, $df = 29$, slope

$= -0.19$, $P = 0.0047$; summer gill net: $r^2 = 0.31$, $df = 31$, slope $= -0.34$, $P = 0.0009$; summer–fall trawl: $r^2 = 0.56$, $df = 32$, P

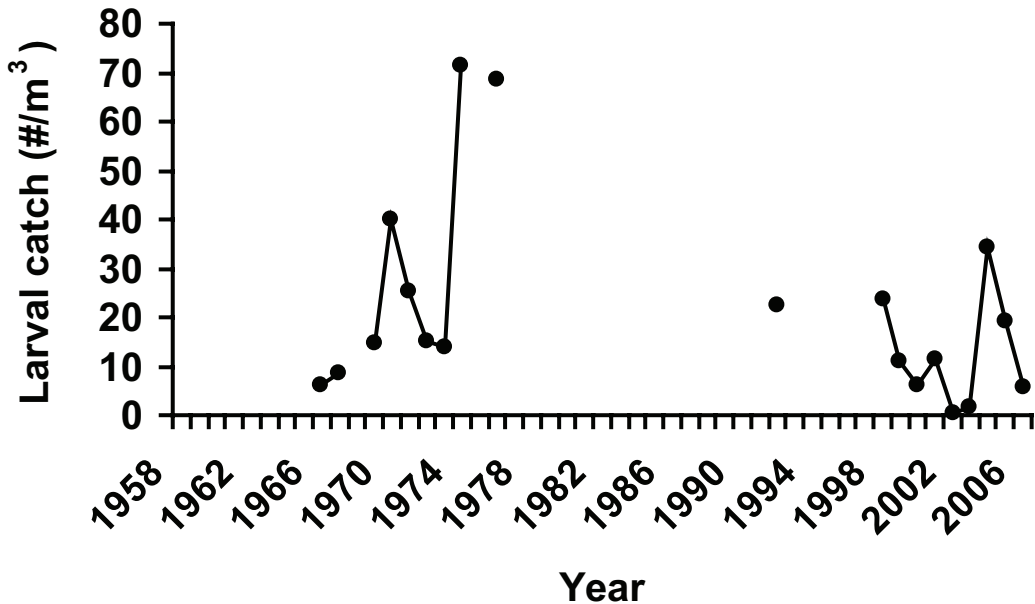


FIGURE 3. Catches of larval burbot in Miller high-speed samplers in Oneida Lake, New York, 1966–2006.

< 0.0001; fall trap net: $r^2 = 0.38$, $df = 21$, slope = -0.42 , $P = 0.0018$).

Bioenergetics analyses suggested that summer conditions in Oneida Lake would result in dramatically reduced feeding rates and energy loss. Bioenergetics modeling predicted that maximum consumption rate of a 1-kg burbot would drop off rapidly as water temperatures rose above Pääkkönen et al.'s (2003) optimum temperature (T_{opt}) of 14°C (Figure 6). Conversely, predicted metabolic costs rose with water temperature, resulting in net energy loss once water temperatures exceeded 21°C , with the deficit increasing until Pääkkönen et al.'s (2003) maximum lethal temperature (T_{lethal}) of 27°C was reached (Figure 6). Seasonal trends in observed diets of burbot in Oneida Lake agreed well with predicted temperature-related consumption rates from the bioenergetics model. Percentage of empty stomachs reached 78% in July samples, when long-term average water temperature was 20.7°C , and peaked at 88% in

August samples, when daily water temperatures averaged 22.1°C (Table 1; Figure 5). Similarly, energy content of burbot livers declined dramatically between spring and fall in samples from 1993 to 1994 (Table 2; Figure 7). Wet weight of burbot livers was observed to decline by almost 80% over the summer, while percent dry weight declined by half and oil content of livers fell from 17% of wet weight to 0, suggesting that more than 80% of the energy stores in burbot livers were utilized over the summer.

Condition of burbot in Oneida Lake was observed to decline during the summer. Length–weight plots indicated that burbot captured in the fall (October–November) were lighter at any given length than those captured in the spring (April–May) and that the difference was more pronounced in samples collected in the 1990s compared to those from the 1980s (Figure 8). Comparisons of relative weights among seasons and time periods provided further evidence that

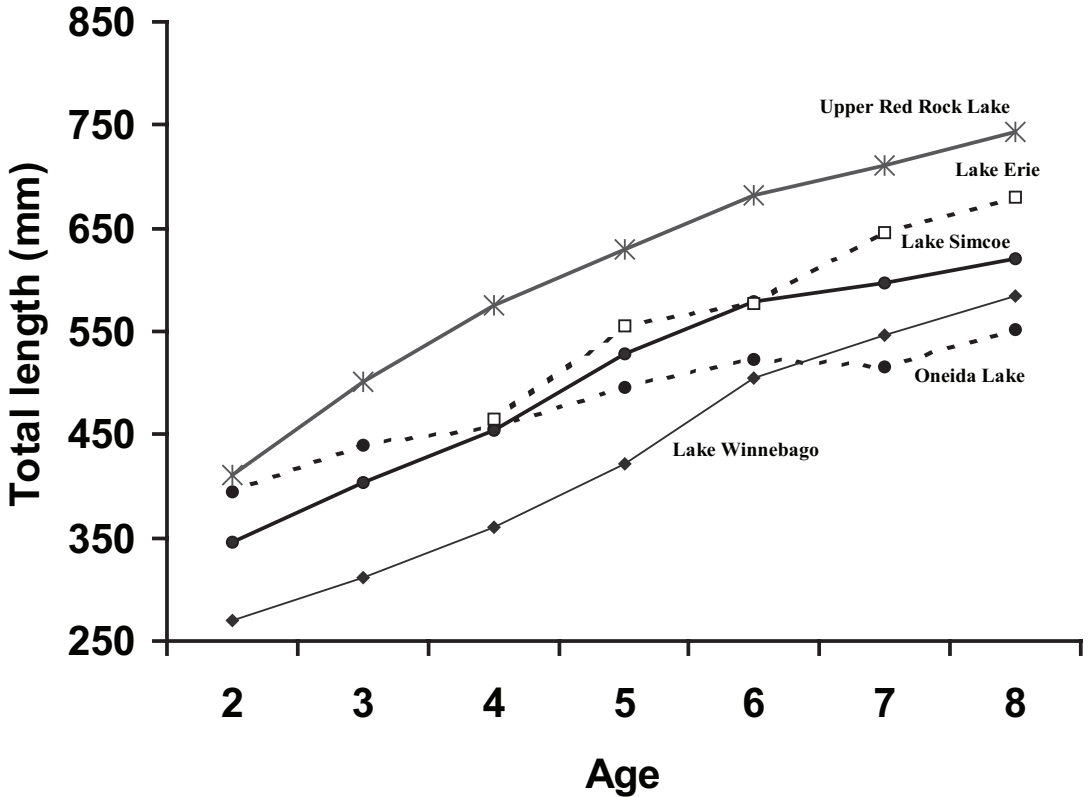


FIGURE 4. Length-at-age of burbot in Oneida Lake, New York as compared to upper Red Rock Lake, Montana (data from Katzman and Zale 2000), Lake Erie, USA/Canada (Clemens 1950b), Lake Simcoe, Ontario (McCrimmon 1959), and Lake Winnebago, Wisconsin (Weber 1976).

condition of burbot in Oneida Lake declined over the summer and that the magnitude of the decline increased in more recent samples (Figure 8). In the 1980s, relative weight declined by more than 10% between spring and fall samples, and this decline was significant (spring $W_r = 121.0$, fall $W_r = 108.7$; Student's t -test: fall $n = 617$, spring $n = 140$, $df = 755$, $t = -7.020$, $P < 0.0001$). Decline in relative weight over the summer in the 1990s was in excess of 21% (spring $W_r = 127.3$, fall $W_r = 104.9$; fall $n = 228$, spring $n = 71$, $df = 298$, $t = -9.949$, $P < 0.0001$). While spring relative weights were 5% higher in the 1990s than the 1980s ($df = 209$, $t = -2.183$, $P = 0.03$), fall relative weights were 4% lower in the

1990s ($df = 844$, $t = 2.796$, $P = 0.005$), confirming that summer weight loss was more pronounced in the 1990s than the 1980s.

The trend towards more severe summer declines in burbot condition in recent decades was consistent with trends in the duration of the period of likely thermal stress experienced by burbot. Bioenergetics modeling predicted that weight loss occurs as water temperatures rise above 21°C , even if burbot were to feed at maximum rates (see above), and the number of days when mean water temperature at 10 m depth was higher than this limit increased significantly over the course of our studies (Figure 9; linear regression of number of days greater than

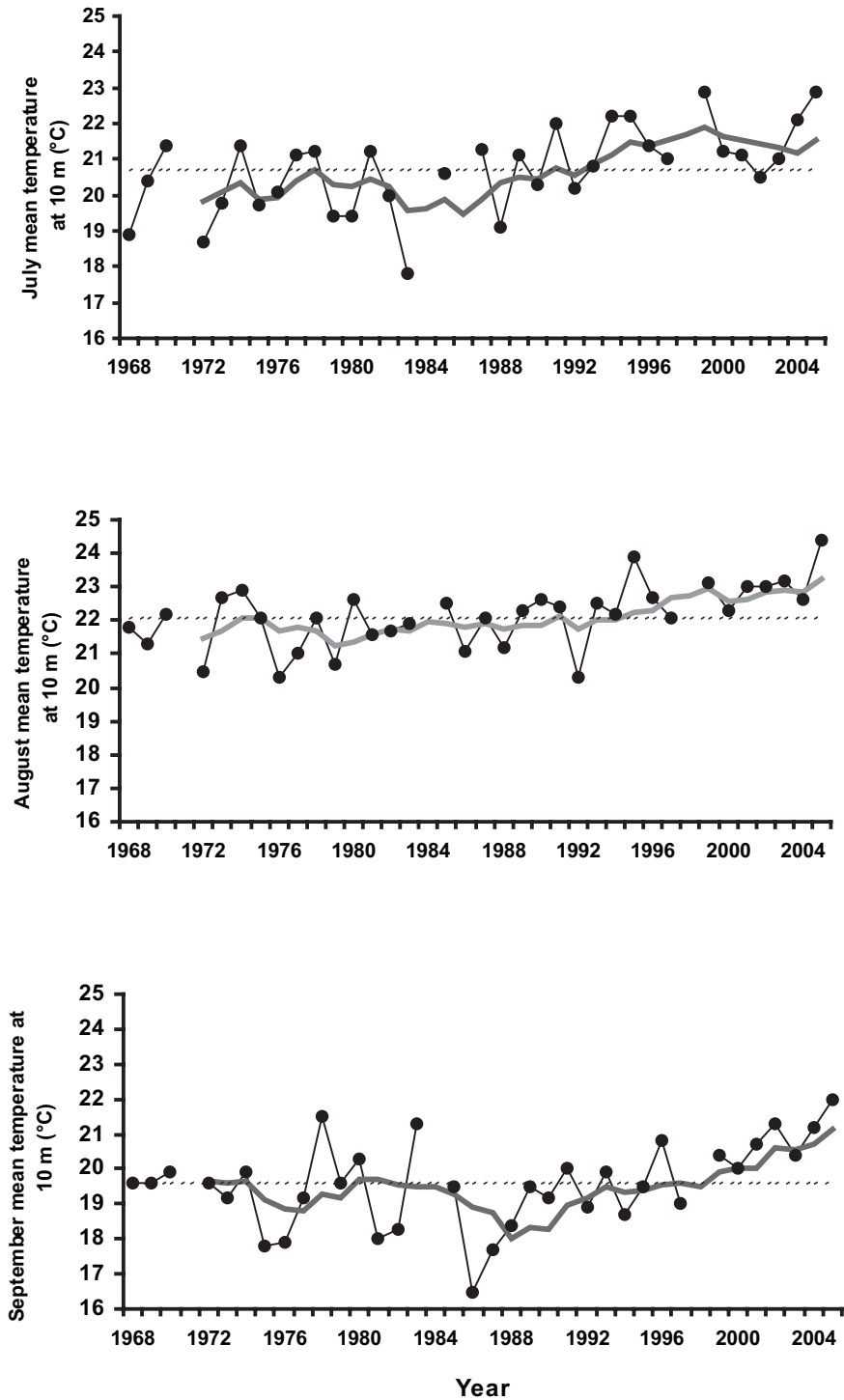


FIGURE 5. Trends in summer water temperatures at a depth of 10 m in Oneida Lake, New York, 1968–2005. Individual year data represented by closed circles and thin line, running 5-year average shown by heavy line, and dashed line indicates mean monthly average for the entire period of record.

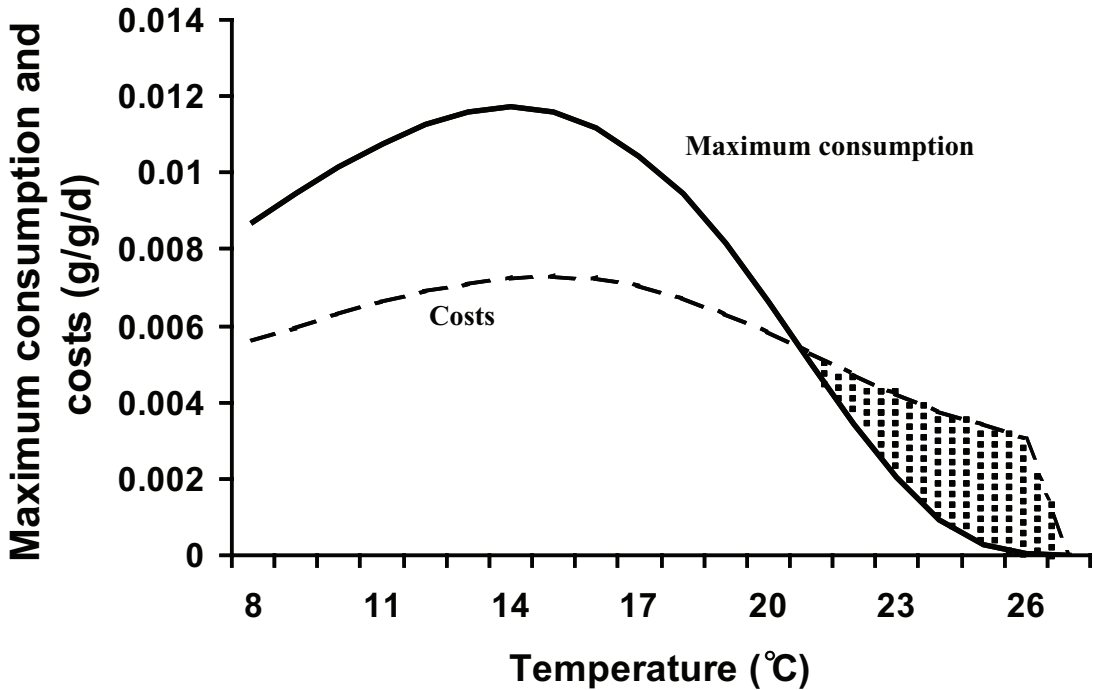


FIGURE 6. Predicted temperature-dependent rates of consumption and bioenergetic costs of a 1-kg burbot. Shaded area indicates temperatures where weight loss is predicted.

TABLE 1. Seasonal trends in diets of burbot captured in trawls, gill nets, and electrofishing in Oneida Lake, New York 1964-1994.

Month	Number of fish examined	Percent with empty stomachs	Percent with fish in diet ^a	Percent with invertebrates in diet
Jan.-March	10	30	40	40
April	13	0	69	69
May	25	16	44	68
June	87	56	18	25
July	65	78	14	5
August	81	88	7	4
September	96	54	43	1
October	77	34	58	4
Nov.-Dec.	17	0	76	18

^a Of identifiable fish in burbot diets, young-of-year yellow perch were the most common (68%), followed by darters *Etheostoma* spp. (11%), young-of-year white perch *Morone americana* (9%), and emerald shiner *Notropis atherinoides* (3%). Other species included trout-perch *Percopsis omiscomaycus*, sculpin *Cottus* spp., gizzard shad *Dorosoma cepedianum*, young-of-year burbot, young-of-year freshwater drum *Aplodinotus grunniens*, young-of-year walleye, logperch *Percina caprodes*, and sunfish *Lepomis* spp.

TABLE 2. Energy density (% dry weight) and water content of livers from burbot captured in the spring and fall 1993-1994, Oneida Lake, New York.

Whole fish		Liver			
Total length (mm)	Wet weight (g)	Wet (g)	% dry weight	Oil content (g)	Mean calorie content (cal/g [SD])
Spring					
576	1,565	112	65	21	7,246 (75)
465	994	137	57	15	7,232 (364)
655	2,277	193	64	48	7,165 (57)
537	1,710	197	65	41	6,878 (276)
460	959	89	66	14	6,449 (682)
635	2,406	246	62	26	6,970 (105)
591	1,735	140	64	30	7,827 (264)
520	1,523	150	65	30	7,173 (1,073)
572	1,430	106	61	15	6,596 (257)
491	894	75	59	9	7,936 (471)
	Mean	146	63	25	7,147
Fall					
602	1,449	22	24	0	7,178 (257)
682	2,136	51	31	0	6,671 (146)
541	1,185	27	40	0	
552	1,086	29	32	0	7,362 (269)
545	1,213	19	31	0	6,735 (1,013)
	Mean	30	32	0	6,987

21°C as a function of year: $r^2 = 0.33$, $df = 30$, slope = 1.05, $P = 0.0006$). The 5-year average number of days in the summer when water temperatures at 10 m exceeded 21°C was typically 40 or less from 1968 through the late 1980s, but that number exceeded 50 in all years since 1995 and reached 70 in 2005. Adult burbot catches were negatively correlated with the 5-year running average number of days that water temperatures exceeded 21°C, and all tests were significant at the adjusted level of $\alpha = 0.013$ for all gears (spring trawl: $r^2 = 0.24$, $df = 29$, slope = -0.01 , $P = 0.0048$; summer gill net: $r^2 = 0.35$, $df = 31$, slope = -0.02 , $P = 0.0003$; summer-fall trawl: $r^2 = 0.48$, $df = 32$, slope = -0.001 , $P < 0.0001$; fall trap net: $r^2 = 0.26$, $df = 21$, slope = -0.02 , $P = 0.013$). Increases were also observed in the number of days that mean water temperature exceeded

22°C ($r^2 = 0.49$, $df = 30$, slope = 1.17, $P < 0.0001$) and 23°C ($r^2 = 0.38$, $df = 30$, slope = 0.63, $P = 0.0001$). The 5-year average number of days greater than 22°C increased from less than 30 in the years before 1988 to more than 40 since 2002, while the average number of days greater than 23°C increased from less than 10 in the years before 1994 to more than 17 since 2002. A mean daily temperature in excess of 24°C was observed on only one occasion between 1968 and 1990, but has been recorded on two or more days in 7 of the last 10 years, with 29 d greater than 24°C recorded in 2005.

Discussion

Long-term trends in catches of burbot in Oneida Lake indicated decreasing abundance

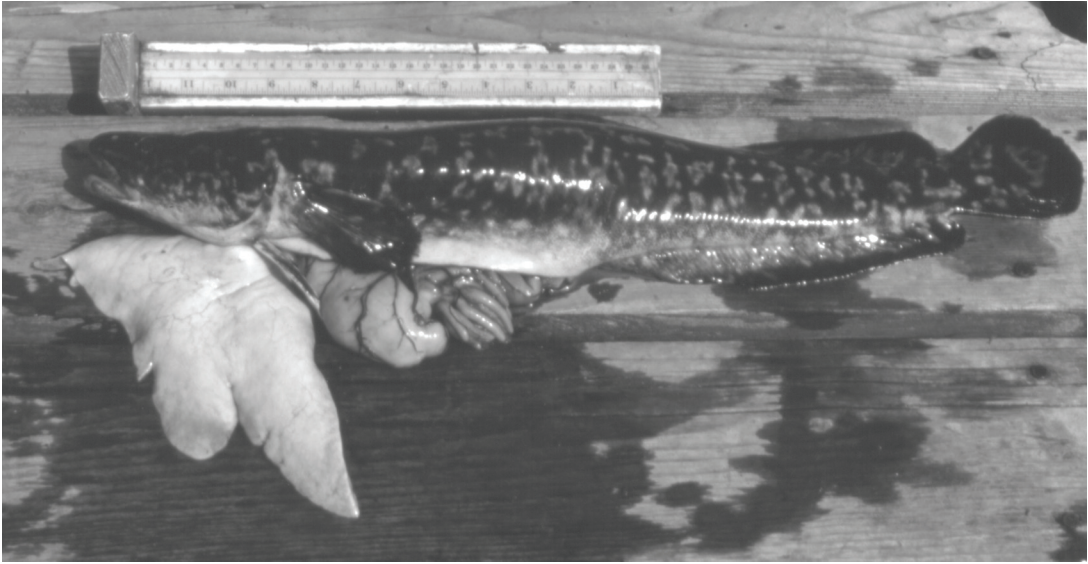


FIGURE 7. Livers of burbot from Oneida Lake, New York in April 1997 (top photograph) and after the summer in September 1997 (bottom photograph).

of adults, particularly in the years since the early 1990s. Spring abundance of larvae has also shown a general decline, although occasional high catches have occurred in recent years. Declines in catches of burbot were significantly correlated with trends of increasing

summer water temperatures in deeper waters of Oneida Lake. Because sampling programs on Oneida Lake do not specifically target burbot, the accuracy of catches as an index of abundance is unknown, but as declines in burbot catches have co-occurred in several

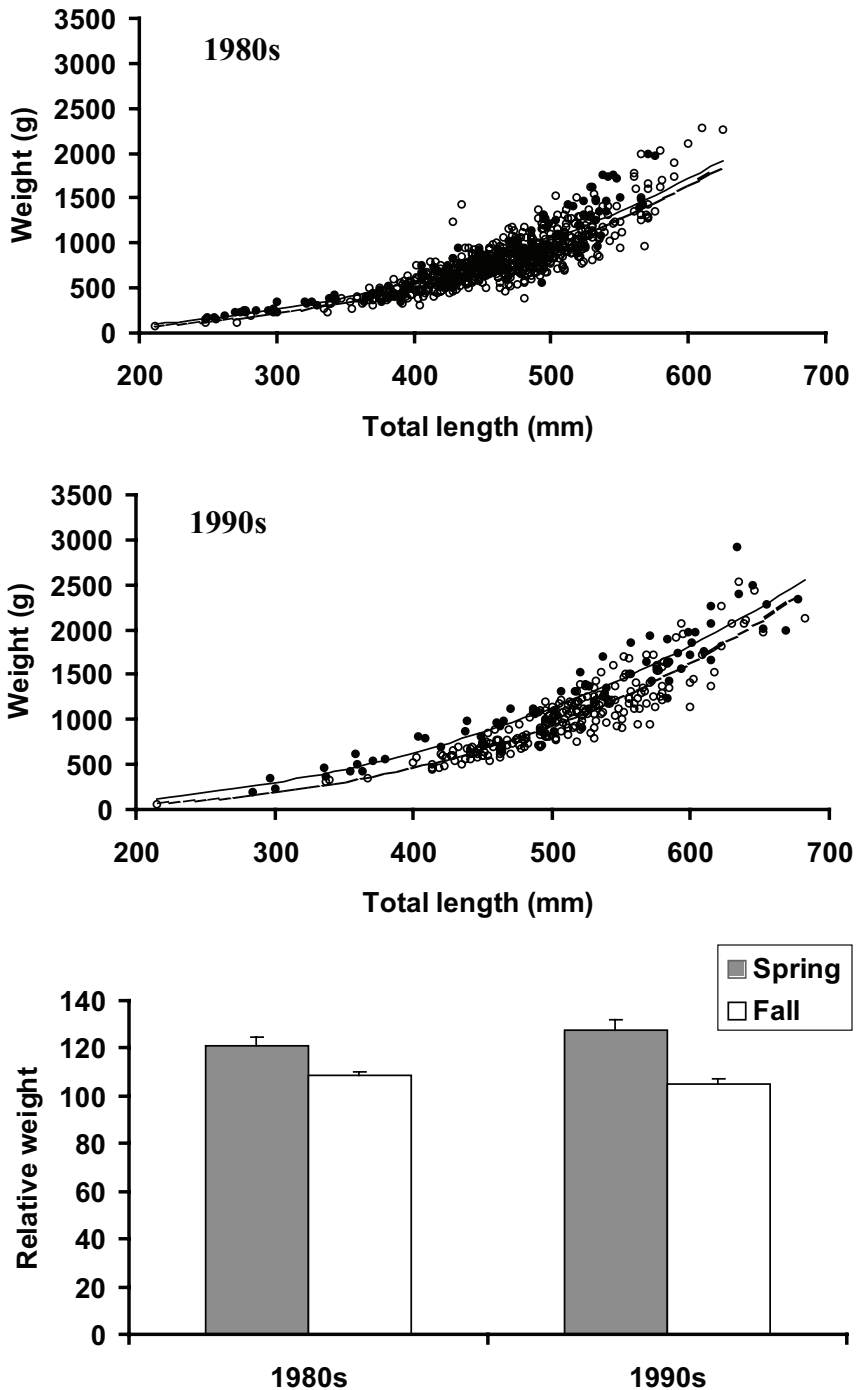


FIGURE 8. Length–weight relationships and relative weights (bottom panel) of burbot captured in the spring (April–May; closed circles, upper line) and fall (October–November, open circles, lower line) during the 1980s (top panel) and 1990s (middle panel) in Oneida Lake, New York. (Length–weight equations: 1980s—fall $y = 0.000004x^{3.1129}$, spring $y = 0.00005x^{2.7009}$ and; 1990s—fall $y = 0.0007x^{2.3072}$, spring $y = 0.000005x^{3.062}$).

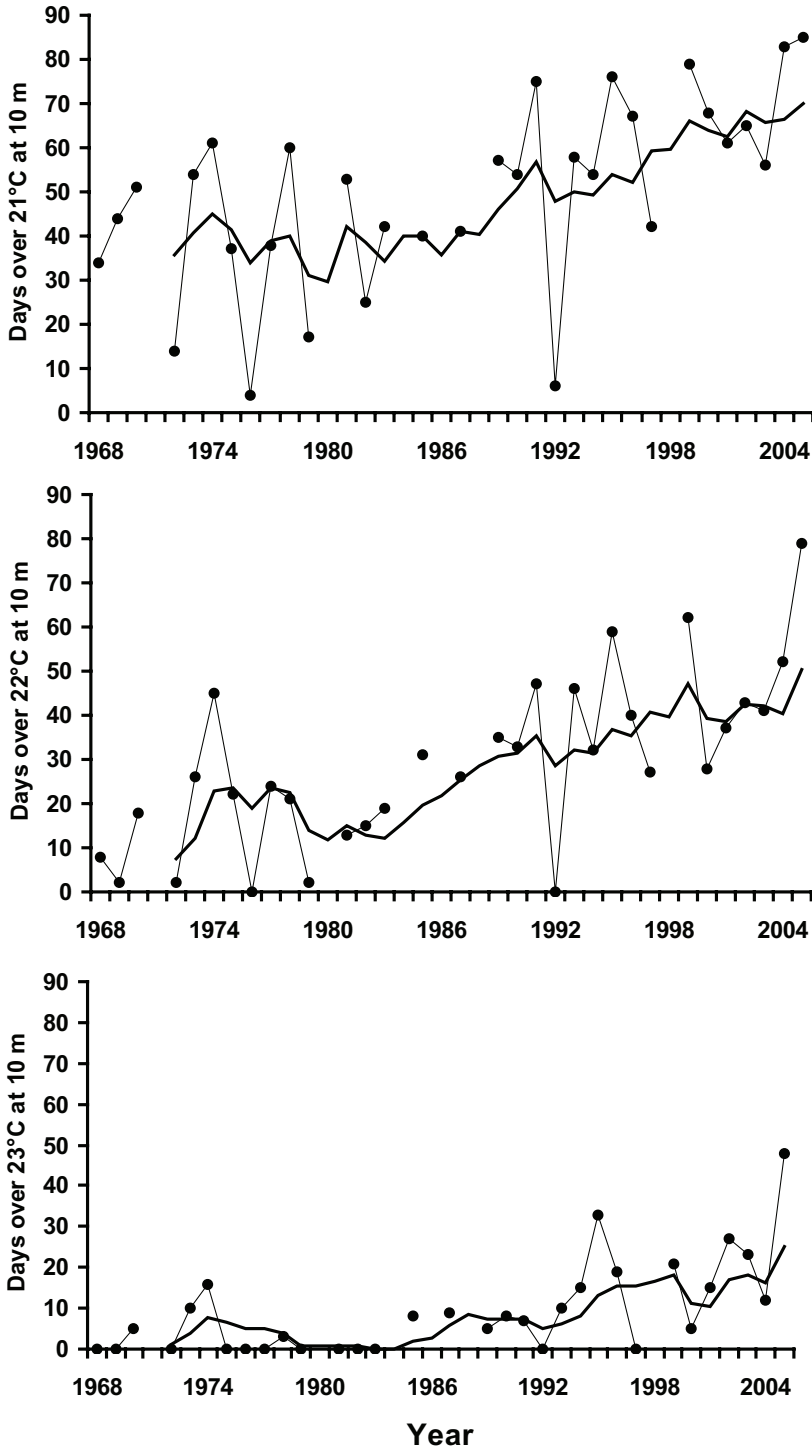


FIGURE 9. Trends in number of days during the summer that exceed levels at which burbot experience thermal stress. Individual year data represented by closed circles and thin line; running 5-year average shown by heavy line.

independent gears, it is unlikely that the observed declines are an artifact of survey design. The correlation between increasing water temperatures and declining burbot catches could stem from other than causal factors. For example, higher water temperatures could reduce burbot activity rates, which would produce declines in summer gill-net catches independent of burbot abundance. However, catches from an active gear (trawl) employed in spring and fall trap-net samples, when burbot activity would not be expected to be reduced by water temperatures, have also declined, suggesting that lower catches are not purely a function of reduced summer activity rates.

Oneida Lake likely always represented marginal habitat for coldwater species such as burbot. Several studies have shown that burbot actively avoid high water temperatures. Edsall et al. (1993), working in Lake Superior, and Carl (1995), in studies in Lake Opeongo, reported that in summer, burbot selected areas below the thermocline where temperatures were less than 13°C. At temperatures greater than 20°C, burbot reduce activity and begin to show signs of stress (Nikcevic et al. 2000; Hölker et al. 2004). With its shallow morphometry and wind-induced mixing, Oneida Lake does not offer the deep, coldwater summer refuges used by burbot in other systems. Even before recent trends towards warmer summer temperatures, burbot were likely routinely exposed to water temperatures in excess of 20°C during parts of the summer in Oneida Lake.

As part of their adaptation to freshwater environments, burbot have developed strategies for coping with brief periods of high water temperatures. Hölker et al. (2004) proposed that when water temperatures reach levels where feeding is reduced or ceases and metabolic costs exceed energy uptake, burbot will utilize energy reserves in the liver to maintain growth and then rebuild liver

reserves in the winter. Our study showed that feeding rates declined through the summer, with the concurrent reduction in liver weight and energy content that would be expected under such a scenario. By the end of the summer in Oneida Lake, livers had decreased in wet weight by 80%, and declines in relative weight in the 1990s exceeded 21%. Increases in the frequency of empty stomachs and reduced volumes of food in burbot during the summer months have been reported from other populations near the southern extreme of the species' range (Clemens 1950a; Robins and Deubler 1955). Hölker et al. (2004) reported depletion of liver energy reserves during the summer months similar to those we observed and also reported reduced condition of burbot following the summer in the River Oder in Germany, where water temperatures can reach 24–25°C. Rudstam et al. (1995) also found increases in the occurrence of empty stomachs and decreases in food volume in burbot diets during the summer in Green Bay, Lake Michigan, but not of the same magnitude as reported from more southern populations. Van Oosten and Deason (1937) did not note strong seasonal trends in a study of burbot diets in the main body of Lake Michigan. Seasonal patterns in energy content of burbot in Lake Superior did not indicate summer declines in a lake with abundant coldwater habitat (Johnson et al. 1999). Reductions in feeding rates and the accumulation of energy deficits appear to be more pronounced in the southern portion of the burbot's range or in systems that lack adequate coldwater refuges.

Evidence of burbot adaptation to warmer water temperatures can be seen in the T_{lethal} of 27°C derived experimentally by Pääkkönen et al. (2003), which is higher than the 24°C value for Atlantic cod *Gadus morhua* that was used in earlier bioenergetics models for burbot (Rudstam et al. 1995). Hofmann and Fischer (2002) found that adult burbot ac-

climated at a temperature of 19.6°C had upper thermal limits of more than 27°C. Pääkkönen and Marjomäki (2000) documented that burbot will still feed at temperatures as high as 23.4°C, although at substantially reduced rates from those observed at lower temperatures. While burbot appear to be adapted to tolerate periods of thermal stress through use of energy reserves from the liver, prolonged periods of high water temperatures would increase the energy deficit that must be made up during the winter.

Our bioenergetics model predicted that weight loss, and presumably use of energy reserves, begins when water temperatures reach 21°C. Hölker et al. (2004) reported reduced feeding at 20°C and documented loss of lipid stores in burbot livers as temperatures rose above this level. Our data show clear trends towards higher summer water temperatures in Oneida Lake in recent decades. The number of days when water temperatures at 10 m depth averaged 21°C or higher in the 1970s through mid-1980s typically averaged 30–40, but in recent years, this period of thermal stress has exceeded 60 d. Moreover, extreme temperatures in excess of 23°C, which were rare in the early years of our data series, now occur with regularity, with more than 2 weeks of temperatures greater than 23°C recorded in 8 of the last 10 years. The observed declines in burbot catches concurrent with increases in the duration of thermal stress in Oneida Lake suggest that prolonged exposure to high temperatures can negatively affect population dynamics.

While our analyses point towards higher summer water temperatures as an explanation for declines in burbot catches, our data do not allow definitive proof of this hypothesis. However, other possible causes for declines in burbot abundance do not appear likely based on our long-term data sets. Burbot are not a targeted species during the winter ice-fishing season on Oneida Lake, but are

caught as bycatch and generally discarded, so in effect there is some winter harvest. Creel data are not available for the entire period of our study, but comparisons of creel data from the late 1950s and recent years do not suggest that changes in harvest of burbot can account for the observed declines in their abundance. Ice fishing effort during the 1957–1959 seasons averaged 3.9 (1 SE = 1.0) angler-hours/ha. During the 1997 and 2002–2005 seasons, effort averaged 3.0 (SE = 0.3) angler-hours/ha (Cornell Biological Field Station [CBFS], unpublished data). Proportion of ice angler catch represented by burbot was higher in the 1950s. While burbot representation in catch was as low as less than 1% during the 1957–1958 season, it reached 6% in the 1959–1960 season and 23% during the 1956–1957 season. Proportion of angler catch represented by burbot never exceeded 1% during the 1997 and 2002–2005 study period (CBFS, unpublished data). Our creel data do not indicate increases in angler effort or angler catch of burbot that would account for declines in the abundance of burbot reflected in our samples.

Another potential factor influencing trends in burbot abundance is the establishment of a breeding colony of double-crested cormorants *Phalacrocorax auritus* on Oneida Lake. Cormorant predation has contributed to declines in populations of walleye and yellow perch in Oneida Lake (Rudstam et al. 2004). However, during the years 1988–2001, while percids were declining, walleye accounted for more than 9% on average of fish identified in cormorant diets and accounted for as much as 42% of cormorant diets in the years immediately following their establishment. Yellow perch accounted for more than 50% of the fish identified in cormorant diets over the same period. However, burbot never exceeded 7% of cormorant diets from 1988 to 2001 and averaged only 1.6% annually of cormorant diets for the entire period.

It is unlikely that this level of predation by double-crested cormorants could account for our observed declines in burbot abundance. Smallmouth bass *Micropterus dolomieu* accounted for a similar proportion of cormorant diets as burbot (1.3% on average for the period 1988–2001), but have exhibited dramatic increases in abundance since the late 1980s (CBFS, unpublished data). Recent cormorant management on Oneida Lake has allowed for increases in the walleye population, but no concurrent increase in burbot abundance has been observed (CBFS, unpublished data).

The mechanisms of the declines we observed are unknown, but it is possible that accrual of large summer energy deficits could impact energy investment in eggs prior to winter spawning. Our larval data indicate that small year-classes have become more common in recent years in Oneida Lake as adult stock size has declined. Morgan and Metcalfe (2001) documented that Atlantic salmon *Salmo salar* will undergo a phase of compensatory or catch-up growth following periods of starvation, but long-term costs of this strategy can include lower lipid reserves, smaller body size, and later maturation. Additionally, even if summer temperatures do not reach levels that are directly lethal to burbot, such environmental stresses and the reduction in condition that accompany them have been shown to reduce resistance to diseases and other pathogens (Wedemeyer et al. 1976).

Our data on burbot dynamics and temperature trends in Oneida Lake provide empirical evidence that supports predictions of habitat loss and range contractions of coldwater fish species that would result from climate change (e.g., Rahel 2002). Summer conditions in Oneida Lake likely always represented marginal habitat for burbot, but adaptations for withstanding periods of thermal stress allowed the population to sustain itself, apparently at high abundances based on early

reports of the lake's fisheries. Historical climate records show that episodes of warm temperatures have occurred as recently as the 1930s, so the Oneida Lake burbot population has endured short-term periods of high temperatures. Warming trends that we have observed over the last four decades in Oneida Lake are consistent with trends in other large lakes (Lofgren 2002). Continued warming could shift Oneida Lake from a marginal habitat for burbot to a system that can no longer support them. Loss of marginal habitats is the first step in predicted range contractions of coldwater species under the current scenario of global warming (Stefan et al. 2001). Our findings illustrate the importance of long-term data sets in tracking responses to environmental change and point to the need for more focused studies of fish populations at the extremes of their geographic range if responses to climate change are to be fully understood.

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